FUNGAL SPORES OF THE GENUS *CTENOSPORITES* FROM THE EARLY TERTIARY OF SOUTHERN ENGLAND

by P. H. SMITH

ABSTRACT. Dispersed fungal spores from Late Eocene deposits from the Hampshire Basin are placed in the genus *Ctenosporites* Elsik and Jansonius. The population studied shows continuous morphological variation between individuals conforming with *C. eskerensis* Elsik and Jansonius and with *C. wolfei* Elsik and Jansonius. *C. wolfei* is therefore placed in synonymy with *C. eskerensis*. Although previously described from Canadian and South Australian Tertiary assemblages, this is the first European Tertiary record of this highly distinctive genus.

THE genus *Ctenosporites* Elsik and Jansonius (1974) has been erected for certain highly distinctive fossil structures of fungal origin. Although first thought to be restricted to the Canadian north-west Pacific and Arctic regions, it has since been shown to occur in an early Middle Eocene deposit from Maslin Bay, South Australia (Lange and Smith 1975a, 1975b). *Ctenosporites* has now been observed in the course of an examination of dispersed fungal spores from the Leaf Bed, Bed X (Tawney and Keeping 1883) of the Lower Headon deposits (uppermost Eocene or basal Oligocene) from Hordle Cliff (Grid reference SZ 262923), Hampshire.

A sufficiently high frequency of occurrence (more than one per thousand fungal spores counted) has enabled comparative studies based upon a large population sample to be made. Description of the morphological variation found, and some comments upon the delimitation of species as described by Elsik and Jansonius (1974) are presented.

MATERIALS AND METHODS

Small samples of matrix were pared to remove the outer surface exposed at the time of collection and thus to expose new faces and minimize the risk of contamination with recent fungal spores. The matrix was treated with concentrated hydrofluoric acid followed by concentrated hydrochloric acid. The dissociated matrix was washed with distilled water and centrifuged several times. The organic material was concentrated by centrifugation in zinc bromide (S.G. 2·2). After further washing, the organic material was mounted in glycerine jelly for microscopical examination.

TAXONOMY

Lange and Smith (1971) have stressed the inherent difficulties in the nomenclature and taxonomy of dispersed fossil fungal spores and have urged that taxonomic distinctions and limits be drawn only on the basis of large-scale population studies. Adequate species circumscription depends upon the availability for comparative study of the

entire continuum of variability. Elsik and Jansonius (1974), in erecting the genus *Ctenosporites*, recognized two species distinguished largely upon the pattern of lateral branching and the shape, if present, of the apical cell of the basal filament. Using the population-study method, the morphological variation present in the Hordle Cliff material appears to have at least three major foci when the pattern of lateral branching is considered. Two of these correspond to those branching patterns already designated by Elsik and Jansonius as separating *C. eskerensis* from *C. wolfei*. The major specific difference, as published, is the tendency of the lateral branches to curve and reach a common level parallel to the apical cell of the basal filament in *C. eskerensis* (text-fig. 4*f*, *h*) whilst the lateral branches of *C. wolfei* (text-fig. 4*c*, *e*, *g*) do not exhibit the same degree of curvature. The tips of the lateral branches therefore do not reach a common level parallel with the apical cell. These two conditions are shown diagrammatically in text-fig. 1*a*, *b*; text-figs. 1*c*, and 4*d*, *j* show the form of branching characterizing the third focus, found in the Hordle Cliff material. Here the lateral branches tend to be more nearly perpendicular to the basal filament than in the first two forms.
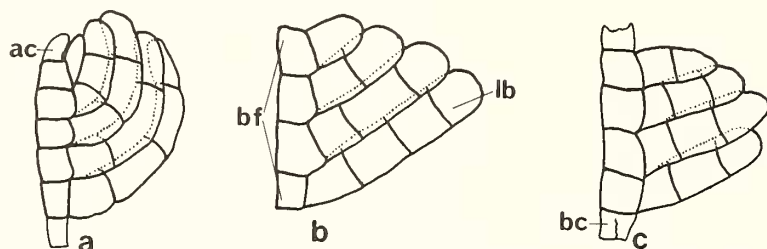
TEXT-FIG. 1. Diagrammatic representations of the branching pattern in *a*, *Ctenosporites eskerensis*, *sensu* Elsik and Jansonius; *b*, *Ctenosporites wolfei*, *sensu* Elsik and Jansonius; *c*, Hordle Cliff form. ac, hyaline apical cell; bf, thickened cells of basal filament; lb, lateral branch; bc, hyaline basal cell.

Whether this variant of branching pattern is sufficient basis to create a third species is highly questionable. Elsik and Jansonius (1974) also place great weight upon the presence or absence of an entire (intact?) hyaline apical cell of the basal filament as a character separating the two species described. In both the Australian material (*see* Lange and Smith, 1975*a*, fig. 1; 1975*b*, fig. 29) and the English material, spores have been found showing the branching pattern of *C. wolfei* but with intact apical cells, calling into question the presence or absence of the apical cell as a sound diagnostic character. The number of non-hyaline, thick-walled cells of the basal filament has also been used to separate the two species, *C. eskerensis* (7 cells) and *C. wolfei* (4–5 cells).

The Hordle Cliff material showed such a wide spectrum of forms, that in order to ascertain whether this could be accommodated in the two described species, measurements of three parameters were made on a sample of 500 spores. The parameters used were the number of thick-walled basal filament cells, the number of lateral branches, and the number of cells in the longest lateral branch. The results of these counts are represented graphically in text-fig. 2.
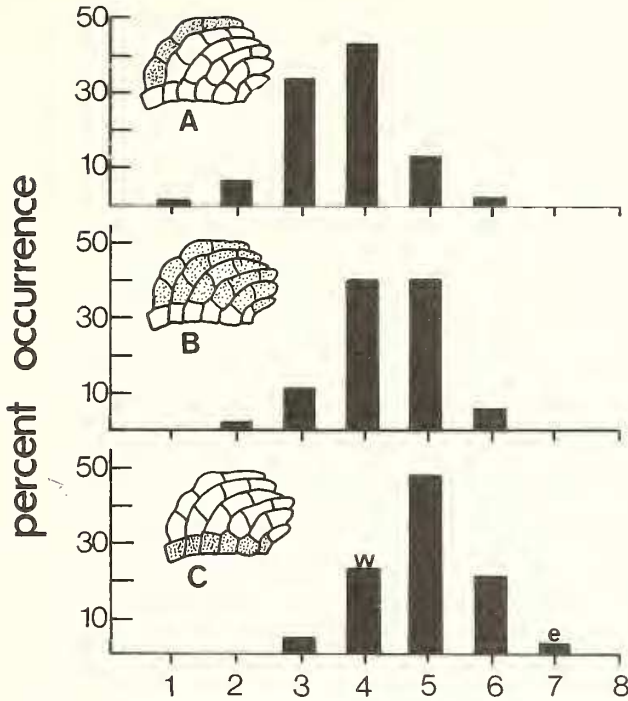
TEXT-FIG. 2. Graphic representation of the distribution of three parameters measured in the Hordle Cliff population: A, number of cells in longest lateral branch; B, number of lateral branches; C, number of thick-walled cells in basal filament. w, *C. wolfei sensu* Elsik and Jansonius; e, *C. eskerensis sensu* Elsik and Jansonius.

The wide morphological variation observed might be accommodated by two alternative taxonomic procedures. One extreme course would be to recognize fifty or so new species, to cover the number of morphological forms observed. Alternatively (and more practically), the generic concept of Elsik and Jansonius (1974) could be accepted, recognizing a single species with wide and continuous variation. The variants within this highly distinctive taxon, although not warranting elevation to specific or subspecific level, are significant enough to warrant cataloguing and illustrating as comprehensively as possible (Lange and Smith 1971, 1975*b*).

Ctenosporites eskerensis (Elsik and Jansonius, 1974) emend.

Type species. *C. eskerensis* Elsik and Jansonius (1974) (p. 957, pl. 1, fig. 1).

Synonymy.

> *C. wolfei* Elsik and Jansonius (1974) figs. 2–4.
> *C.* cf. *wolfei* Lange and Smith (1975*a*) fig. 1.
> *Ctenosporites* sp. Lange and Smith (1975*b*).
> 'Unidentified fungi', Hills (1965) plate 15, fig. 16.

Emended diagnosis. Multicellular structure of fungal origin; basal (main) filament consisting of a variable number (3–9) of thickened cells; with or without a more hyaline basal (attachment?) cell; apical hyaline

cell may be present; lateral filaments, although always more or less parallel to one another, showing varying degrees of curvature towards apex of basal filament; lateral filaments usually decreasing in septation from base to apex of basal filament.

Discussion of Hordle Cliff material. The specimens figured as text-figs. 3*a–e* and 4*a* are interpreted as immature forms, due to the relative lack of thickening of the basal filament cells. Corresponding forms from the South Australian material are illustrated by Lange and Smith (1975*b*, figs. 1 and 21).
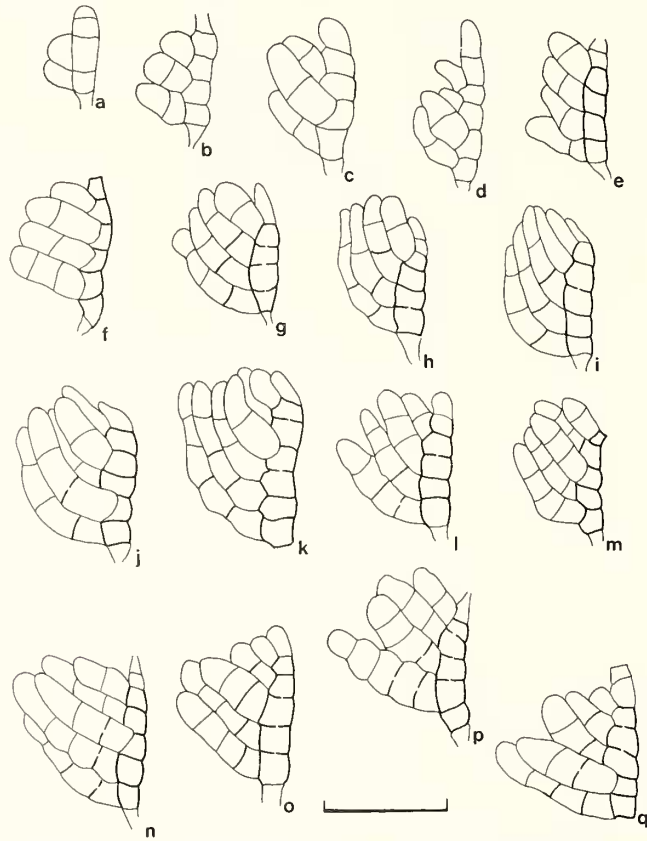
TEXT-FIG. 3. Camera lucida drawings of variation in spore morphology shown in Hordle Cliff population. Scale bar, 25 μm.

The specimens shown in text-figs. 3*h, k* and 4*f, h* correspond to the species *C. eskerensis* (*senso strictu*) as originally described by Elsik and Jansonius (1974). That shown in text-fig. 3*l* would have been placed in *C. eskerensis*, due to the presence of an intact apical cell, whilst that shown in text-fig. 3*m* would have been designated *C. wolfei* due to the lack of an intact apical cell. Text-fig. 3*o, p* shows forms which have lateral filaments almost perpendicular to the basal filament but differ in the presence of an intact, or broken apical cell, whilst text-fig. 3*q* differs only in the absence of an apical cell and in possessing a thin-walled penultimate basal filament cell.
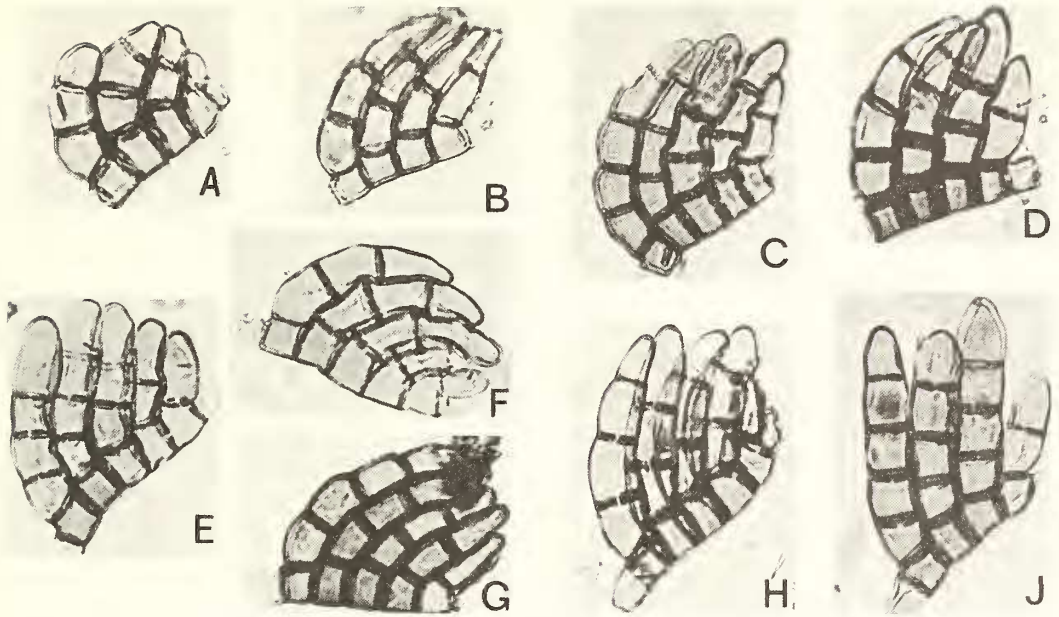
TEXT-FIG. 4. Photomicrographs of some morphological variations found in Hordle Cliff material. Magnification ×1000. Specimens illustrated in text-figs. 3 and 4 are from slides V58924–V58926, deposited in the British Museum (Natural History).

Although the majority of the forms observed in the Hordle Cliff material are characterized by the unilateral branching pattern, several structures were found which correspond to the form illustrated by Lange and Smith (1975*b*, fig. 10). This particular form, or a closely similar structure, has also been catalogued and illustrated as 'Fungal Spore A' by Clarke (1965) from Upper Cretaceous deposits from Colorado. As stated by Lange and Smith (1975*b*) this form is probably a member of the genus *Ctenosporites* but, due to the possession of a branching pattern which is not unilateral, it cannot be assigned to the genus as it is presently delimited.

CONCLUSION

The occurrence of *Ctenosporites* in deposits from the Hampshire Basin widens the recorded distribution of the taxon within early Tertiary floras whilst still maintaining a stratigraphic restriction to the Eocene and Oligocene Periods. Although no modern fungal genus has been shown to have spores with the characteristic unilateral branching of *Ctenosporites*, it is thought to have affinities with the conidia of the saprophytic dematiaceous hyphomycete *Dictyosporium*, which are branched, cheiroid spores usually flattened in one plane (Ellis 1971, fig. 25, p. 56). Conidial stages of *D. toruloides*, figured as *Speira toruloides*, from dead wood, herbaceous stems, and occasionally leaves, in marsh and fen conditions (Ellis *et al.* 1951), show a certain degree of similarity with the branching pattern of *Ctenosporites*. The lack of host-specificity

in *Dictyosporium* (Ellis 1974) corresponds with the apparent lack of host specificity already noted for *Ctenosporites* (Lange and Smith 1975*b*).

The inclusion of such a wide variation of spore morphology within a single species is justified by an examination of extant species of Fungi Imperfecti. A similar range of variation is often found within the spores of a single species. Underlying causes of this variation have been shown to include such environmental factors as the nutritional status of the substrate. Brown and Horne (1926) demonstrated that in *Fusarium* species a low carbon/nitrogen ratio led to the production of short spores with few septa; and conversely that long spores with increased septation resulted from a high carbon/nitrogen ratio in the substrate. Although the mode of nutrition, either parasitic or saprophytic, cannot be inferred from dispersed spores, the apparent lack of host-specificity in *Ctenosporites* could well be a contributing factor in the wide range of spore morphology observed. If *Ctenosporites* was an element of a floristically diverse community, this would present a large number of alternative substrates with correspondingly variable nutrient levels available for utilization. Substrate variability could be a contributing factor in the morphological variation of the mature spore of *Ctenosporites*.

This first European record for *C. eskerensis* broadens the known distribution of this taxon and, as with the previous records, other fungal remains found in association with this spore type are indicative of moist, warm, climatic conditions. The fungal remains thus bear out the earlier conclusions of Reid and Chandler (1933) and Daley (1972) that higher rainfall and elevated temperature characterized the Palaeogene climate of southern Britain.

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